

2 Neither warm and moist, nor cold and arid: the ecology of the Mid Upper Palaeolithic

The later part of the Middle Weichselian was an episode of climatic instability with short, staccato oscillations with reduced impact on the generally open, steppic environment: a less intense version of the Mammoth Steppe with a rich biodiversity, occupied by nomadic, wide-ranging large mammals such as woolly mammoth, bison, horse, woolly rhino, reindeer, saiga and the large carnivores lion, wolf and spotted hyena. The Mammoth Steppe environment from Western Europe to Alaska, although very coherent, showed an increase in species diversity from north to south and the maximum number of mammal species occurred in mountainous areas.

1. Introduction

As during all episodes involving many thousands of years, the climate during the Mid Upper Palaeolithic (roughly 30,000-20,000 years ago) was quite variable. In fact, it is that variability which might provide the core insight to the overall mean character of the ecology of that time. Climatic modelling depends on a reasonable steady-state interannual situation, for example the extremes of the generally warmer/moister Holocene or the colder/arid Last Glacial Maximum (LGM). The late Middle Weichselian was neither. In fact its character may be best captured by a model of climatic instability which was responsible for holding the vegetation and faunal composition at some imaginable mean, oscillating around a set-point that was neither the warmer moist Holocene nor the cold and aridity of the LGM.

That being said, the proxy details of the European pollen record, invertebrate and mammalian fossils, loess deposition, and glacial extent suggest that the environment was generally much more open, tending toward steppic, than most modern biomes distributed across Europe. It was virtually treeless yet seems to have been tolerated by a diverse assortment of mammalian species, and of course palaeolithic people. This was not true during the LGM, during which time the European human population was limited to a more southern distribution (see also Street and Terberger, this volume).

Thus it seems to have been a time of amelioration of the Mammoth Steppe base-line, yet retaining much of its open-ground character. If all that is a fair generalisation, then we could profit from looking at the mechanisms maintaining the

Mammoth Steppe and see what kind of potential ameliorating elements can be found.

2. Climatic mechanisms for the Mammoth Steppe

2.1 MEGACONTINENTAL ARIDITY

Evidence for an intense aridity is clear during glacial periods (Hopkins *et al.* 1982; Vrba *et al.* 1995), though its causes on such a megacontinental scale have been clouded in ambiguity. In the far north, aridity during the LGM would have favoured plants which today persist in the north only in the most limited habitats, such as south-facing steep slopes, or other local, especially arid locations and in the southern steppe communities. We need to imagine a late Pleistocene environment in which the tables were turned, with mesic-adapted biota found only in uniquely damp situations and arid-adapted species dominant and widespread. However, the picture emerging is not just a matter of proportional changes from mesic to arid, but one so extreme that many mesic-adapted forests, forest successions, and forest floor animals and plants were driven to regional extinction throughout the north, from Western Europe to Alaska. The northern perimeters of the distributions of many of these plant and animal species, which are dominant northern species today, were, in the late Pleistocene, thousands of kilometres to the south, such as for instance polar fox (*Alopex lagopus*), reindeer (*Rangifer tarandus*), collared lemming (*Dicrostonyx*) and true lemming (*Lemmus lemmus*) (Markova *et al.* 1995).

2.2 FORCES PRODUCING ARIDITY

Various workers (Hopkins *et al.* 1982; Bartlein *et al.* 1991; Ballantyne and Harris 1994) have treated the specific causes of this cold-arid northern environment during Glacial times, attributing them in a direct way to periglacial effects and the changing earth-sun geometry of Milankovich insolation cycles. But proximate causes were a combination of features; of these, there is an unrecognised, proximate key element throughout the north which seems to have been crucial, a much higher frequency of clear skies than seen today (Guthrie in press). This enhanced evapotranspiration in summer (aridity) and radiation deficit to the black night sky in winter (cold).

2.3 ORIGIN OF THE MEGACONTINENTAL MAMMOTH STEPPE

The ultimate forcing agents of Pleistocene changes are hotly debated, *centring around CO₂ atmospheric concentrations, solar input, oceanic current directions, and many other elements*, all of which seem to change in synchrony with the climatic shifts. In the minds of many Quaternary climatologists (Partridge *et al.* 1995), tectonism seems however to be the main frontrunner theory in this controversy (Manabe and Terpstra 1974). Mountain uplift occurred in many continents during the Quaternary, but nowhere was this more pronounced than in Central Asia, which also concerns us here as it seems to have been responsible for much of the aridity of the Mammoth Steppe. Throughout the Tertiary the Indian Plate was driving into southern Asia, creating the largest mountain range in the world. Apparently, the rate of uplift increased during the last 2.5 million years, and especially during the last million (DeMenocal and Rind 1993). As a result, *the mountains of the Tibetan Plateau reached their greatest height, and produced their greatest climatic repercussions in blocking atmospheric flow from the monsoons of southeast Asia* (Ruddiman and Kutzbach 1989). This orography was responsible for maintaining both the Siberian-Mongolian high pressure and Aleutian low pressure systems in their present locations (Manabe and Terpstra 1974; Ding *et al.* 1992). A core of extreme aridity developed in the blocked monsoonal shadow.

From Western China and Mongolia this core of aridity now extends far to the West and East. However, during the Pleistocene this steppe at times extended much further and it apparently expanded and contracted in synchrony with the Milankovich cycle. A strong winter monsoon is needed to intensify the Siberian-Mongolian high-pressure system; *winter monsoons seem linked to intensification of clear skies and cold in the far north* (An *et al.* 1995). It is also likely that the intensity of the Siberian-Mongolian high is strongly associated with northern hemisphere ice cover (DeMenocal and Rind 1993; Chen *et al.* 1997). During the Milankovich-predicted low-insolation times, when aridity in Northern Asia intensified (Chen *et al.* 1997) and extended west into Europe, and eastward into northeastern Asia, the landscape took on a quite different character. It became a cold steppe, underlain with permafrost, and dominated mainly by cold-tolerant and arid-adapted species, including mixes of lion, horse, antelope, and rhino combining with collared lemming, arctic fox, reindeer, and muskoxen (Guthrie 1990). Invertebrate fossils also exhibit unusual mixes of species (Berman and Alfimov 1997).

Palaeoclimatic reconstructions of atmospheric flow (see discussion in Soffer and Gamble 1990) point to a latitudinally stable eastward flow of the winter (January) storm track across Europe at about 47° N latitude between

the Scandinavian ice sheet and that of the Alps, continuing on that latitude directly across Asia just north of the Tibetan Plateau. This runs down the West-East bore of the Mammoth Steppe. *All the data on direction of loess deposition agrees with this* (Porter and An 1995).

So several geographic features seem to have worked in a complimentary way to exaggerate the periodic spread of the cold steppes out of central Asia, during Milankovich low-insolation times both by limiting moisture and by promoting clear skies:

- (1) *the driving force for the core Asian steppe was an enormous and stable high pressure system north of the Tibetan Plateau;*
- (2) *deflection of the larger portion of the Gulf Stream southward, past southern Spain onto the coast of Africa, reduced temperatures (hence moisture and cloud cover) that the Atlantic current brings to Western Europe;*
- (3) *growth of the Scandinavian ice sheet created a barrier to North Atlantic moisture;*
- (4) *likewise, the icing over of the North Atlantic sea surface with reduced flow of moisture over northern America from the east;*
- (5) *the latitudinal winter (January) storm track seems to have swept across Eurasia;*
- (6) *lowered sea levels exposed a large continental shelf to the north and east of the American continent, producing a vast northern plain, which increased continentality to the north;*
- (7) *in the very Far East, North American glaciers shielded interior Alaska and the Yukon Territory from moisture flow.*

These physical barriers to moisture flow created a vast arid basin or protected 'inner court' spanning parts of three continents. Undoubtedly innumerable local effects would have shaped local conditions and created special situations, but the coherence of the Mammoth Steppe was much greater than local influences, particularly the local effects of ice sheets.

3. The 'no-modern-analogue' phenomenon

3.1. UNUSUAL ASSOCIATIONS

Throughout the 1970's and 80's there was a revolution in palaeobiologists' thinking. Data began to show that past communities, even from the recent past, were often composed of species not found in association today (Storch 1969; Davis 1981; Guthrie 1990; Van Kolfschoten 1995). We came to realise that biomes were not reacting to climatic change as units but as individual species. Response to climatic changes was *surprisingly individualistic with unexpected species differences*. Our faunal and floral evidence revealed species mixes for which we could find few or no modern analogues.

Obviously, these 'no-analogue' associations can be overemphasised and misunderstood. In part, it is a metaphor for saying that biomes do not move around lock-step through time. This concept does not mean to suggest that there are never any valid analogues between the present and past, we would be nowhere without them; the past coexistence of reindeer (*Rangifer*) and saiga (*Saiga*) is informative to our imagination because of the information we can draw from them individually in the present, despite their non-overlap today (Sher 1968; Guthrie *et al.* in press).

There are patches of steppic communities in north-central Asia, some quite expansive, which are scattered into boreal habitats, which do provide some rough analogues to the Mammoth Steppe. In North America there are rare, but similar situations, particularly on steep south-facing slopes. These steppic islands in the ocean of tundra/boreal forest help researchers better understand the tension of forces that produce particular biotic associations and physiognomies (Wesser and Armbruster 1991). Taking the extreme no-analogue position is a little too close to 'Geological Postmodernism'. It is certainly a truism that the co-variance of many species' responses to varying climates is high, and some species pairs are their own interdependent variables - forest floor species which are obviously dependent on the special environment that forest species create. These co-covariant clusters mean that biomes are real coherent entities, in degree. But it is this 'degree' aspect which gives us caution and perhaps insights.

The vast Pleistocene steppe seems to have had a high degree of unusual associations, particularly during Oxygen Isotope Stage (OIS) 3, not only in terms of species composition but also novel assemblages above the level of the community. Pleistocene biomes were different and some apparently had an overall physiognomic character unlike any today.

3.2 THE PROBLEM OF MODERN ANALOGUES ON SUCH A MEGA-CONTINENTAL SCALE

Plants are limited in the polar extremes by the short cold summer. Cwynar and Ritchie (1980) and Colinvaux and West (1984) were certainly right in saying that a barren and unproductive polar desert could not support a complex large mammal community, such as was described for the Mammoth Steppe. This led them into the wrong horn of a dilemma; if it was a polar desert then there were no large mammals. But the large mammals were there, it was not polar desert. The evidence for the over-all character of the biota of the Mammoth Steppe is remarkably different than that of polar deserts.

This misconception points out the mistake of trying to reconstruct northern and mid-latitude palaeoecology during glacial episodes by simply making it colder. Of course, cold is important in our reconstruction; yet summer LGM

Milankovich insolation values are only a little different from modern values (Berger 1978). Exactly why it was cold is an interesting problem, but the answer to that problem may not alone explain the aridity.

It is one thing to reconstruct a past comprised entirely of species that are extinct, a Jurassic Parkland, for example, but it is almost an even greater stretch for the imagination to reconstruct a past environment which includes extant species but in peculiar associations and habitats. It is still counter-intuitive to imagine reindeer, cheetah, muskoxen, hyena, leopard, rhino, horse, ibex, sheep and arctic fox living together. The same is true for the smaller mammals: for example the arctic lemming (*Dicrostonyx torquatus*), now living in the far north (north of 60° N) and the steppe lemming (*Lagurus lagurus*), nowadays widely spread over arid steppes and semi-deserts without permafrost in the area between 45° and 55° N, lived together in for instance southern Germany during episodes of the Late Pleistocene.

4. Nutrient vs. moisture limitations

Because of the present-day flow of the Atlantic current and the resulting flow of moisture across Europe, nutrients are in shorter supply than moisture: from both a physiological and ecological view we can say that nutrients are more limiting than moisture. Spreading standard garden fertiliser (Nitrogen, Phosphate and Potassium) in almost any northern landscape creates a startling effect (perhaps with the exception of a mature closed-canopy coniferous forest). This dose of nutrients changes the species, transforms plant growth, and greatly changes overall appearances of the site. The same is not quite true of moisture. Van Cleve *et al.* (1983) found that, with some exceptions, nutrients and temperature controlled both the type and productivity of taiga forests, not moisture.

5. The problem of 'periglacial effects' at a time when there were no glaciers

Historically, our understanding of the communities of glacial-age biota began in Europe (see review by Ballantyne and Harris 1994). In northwestern Europe the landscape effects of a cold climate (widespread cryogenic geological features, elimination of even cold-tolerant woody plants, expansion of the 'woolly' mammals, and so on) were directly linked to glacial proximity. But this conflation of glacial proximity and biota seems to have created a general misconception about 'periglacial' matters. The cold-arid character and extent of the Mammoth Steppe is more complex than simple glacial proximity. Vast areas of Asia many hundreds or even thousands of kilometres from significant glacial proximity still exhibit features similar to 'periglacial' landscapes.

The word 'peri' implies adjacency, like standing next to an open refrigerator door. Although the large ice masses

certainly had a profound effect on weather tracts and moisture depletion, attributing the Mammoth Steppe simply to 'periglacial effects' does not let us understand the complexity of large-scale forces which were responsible. 'Periglacial' could be used appropriately in certain situations where it may actually apply, but on the whole it is an outdated concept built on a misconception and we are better off without it. Certainly, it is of little help to us studying the Gravettian, because the northern ice sheets were quite reduced, yet the landscape still retained aspects of the treeless Mammoth Steppe.

6. Climatic-ecological variations in the late Pleistocene and their implications for the Mammoth Steppe

Climatic proxy information from such sources as North Atlantic marine cores (e.g. Shackleton 1987; Bond *et al.* 1993; Kotilainen and Shackleton 1995), Greenland ice cores (e.g. GRIP 1993), China loess chemistry (e.g. Porter and An 1995; Chen *et al.* 1997), and others have shown larger fluctuations within isotope stages and across a number of different time scales than data had once portrayed, and our earlier models had projected. This is particularly true for OIS 3, and within the later phase of that period, corresponding to the Gravettian. While the variability seems almost globally consistent, the set points across the north are quite different. These variations are particularly significant with regard to the Mammoth Steppe habitats. For example, trees invaded far northward in Siberia and Alaska during OIS 3. Yet in Europe most tree species were trapped beyond the southern mountains (Pyrenees, Alps, and Carpathians) (Van Andel and Tzedakis 1996). This did not mean that in OIS 3 steppic Europe continued to experience peak LGM conditions. For example, during this Interstade (OIS 3) hominids were able to penetrate far north towards northern Russia (Pavlov and Indreliid, this volume) and they inhabited southern England (Pettitt, this volume; Roebroeks, this volume). Likewise, large mammal faunas from Central and Northwestern Europe were more complex and species-rich during OIS 3 than during OIS 2 and 4 (Stuart 1982). That is also true for the smaller mammal faunas, as can be deduced from the OIS 3 smaller mammal fauna from the Sesselfels Cave (southern Germany) (Van Kolfschoten and Richter, in prep.). This same pattern is seen in northeastern Asia and even as far north as Alaska, where during OIS 3 the mesic-arid adaptive spectrum was also very scrambled. As a diagrammatic example, radiocarbon dates from the extinct, mesic adapted, browsing stag-moose, *Alces latifrons*, are contemporaneous with dates from fossils of saiga, *Saiga tatarica*, a much more arid-adapted species, in the very same fossil localities (Guthrie *et al.* in press).

However, one has to be aware of the geographical variation in the diversity of the mammal fauna. The species

richness during the Bryansk Interstadial (35,000-24,000 bp) varies from about 10 mammal species in the northeastern part of Eurasia to 33 in the south. The highest number of species can be observed in mountainous areas like the Urals, the Caucasus and the Carpathians (Markova *et al.* 1995).

Overall the Eurasian palaeoecology appears to have been a mix of riparian fingers of woods, but few forests, and uplands covered with a variety of arid tolerant plants and animals (Van Andel and Tzedakis 1996). That is, these steppic species lived within a community enriched by a few, more mesic species. We encounter a complex of ecological associations without extensive modern analogue. But remember, the marine cores, the Greenland ice cores, and deep Chinese loess sections show tremendous climatic variations for the northern hemisphere in the Late Pleistocene – it was not a smooth pattern (see Chen *et al.* 1997 for a comparison). What all this variation meant on the ground is certainly not clear. Did species proportions fluctuate wildly from one century to the next? There would be every reason to predict as much, especially for species near their margins of ecological tolerance.

7. Maintenance of Mid Upper Palaeolithic biotas by short periodic staccato of climatic jerks

New evidence suggests that the virtual presence of a large ice-free area in Fennoscandia during the Middle Weichselian (Ukkonen *et al.* 1999) did not bring back interglacial woodlands to Europe. The increased flow of moist air across Europe from reduced glaciation and reduced frozen seas is not sufficient to explain the special open European landscapes during OIS 3. What could then have been the cause? New climatic proxy information highlights saw-tooth climatic switches at shorter time-interval scales, but we know that most biotic changes require some lag time (for example, several thousand years for trees to move northward). Cold-arid snaps on micro, meso, and macro scales could present us with a vegetation not adapted to the mean temperature-moisture regime. It is probable that extreme conditions during the short span (say, 100 years) of one sharp saw-tooth climatic episode may be sufficient to restart (back to zero) time-transgressive changes which would have required thousand(s) of years to complete. However, before that time another short saw-tooth episode may again set the clock back to zero. Thus, it would be possible to maintain a climatic mean of one condition and have many proxy species behave as if it were another. For example, across much of Europe, during OIS 3, it may have been generally warm and wet enough for sylvan elements to re-colonise from the south, but irregular and infrequent episodes of clear skies, and the aridity it produces, kept them out. This kind of phenomenon may have happened widely in the deep past. The causes of

this variability may be complex: fluctuations in the Atlantic current, jet-stream shifts for example in the pattern of the winter storm track, or other factors.

8. Human implications of the staccato climatic model

Presuming the record is correct, that the period at stake was a much more climatically unstable time, marked by episodes of rangeland failures sandwiched between long episodes of thick sward richness, life would have been different than during earlier or later times. Human populations would have probably expanded and declined commensurate with their resources. Ecological instability is not necessarily bad for an opportunistic facultative strategy that is fast to respond to rapid and major changes.

In general these changes would have selected for large herbivore behaviour which was less territorial and more nomadic. The nomadism would have resulted in large herds moving through unfamiliar terrain. We know this to now characterise saiga antelope, reindeer, and bison when numbers are large. This potential mobility probably was true for horses as well (the caballoid switch from territoriality to a mobile harem seems to have been a part of that adaptation requiring less attachment to local landscape). This high mobility of large herds would have presented considerable opportunity for large mammal hunting specialists, even though fraught with uncertainty and unpredictability. Frequent back-ups of other supplemental and secondary resources may have been the result. Indeed this is what some of the archaeological sites show.

9. Mammalian biomass during the Mid Upper Palaeolithic

It is not possible to reconstruct mammalian biomass from the fossil record. That being said, one can use modern analogues as rough guidelines to imagine some rough parameters. If we assume that large mammals were important to Upper Palaeolithic economies (this does in no way reflect on the fact that in many instances diverse supplements of other resources were used seasonally), it is relevant to discuss large mammal biomass. Mature woodlands, such as those characteristic of the Holocene of Europe, support relatively low mammalian biomass. The forage is simply out of reach of most large herbivores and the understory is not very productive and also it is heavily defended against browsing. Likewise, the vast arid, Eurasian steppes of the LGM, while extensive, was not very productive.

But, what if some facies of the steppes were maintained by episodic severe weather while the actual mean year was moderate in terms of cold and aridity? One could then predict that the forage would have been at higher concentrations, probably in the kinds of plant species, which

were most nutritious. The proxy evidence is straightforward that overall Europe was occupied by a less intense version of the Mammoth Steppe. The result of this would have been a higher standing biomass of large mammals. The increased diversity of European species during OIS 3 lends support to this hypothesis.

Though this less intense version of the Mammoth Steppe dominated most of Europe, the actual sward species composition undoubtedly varied considerably from region to region. In other words there was much internal variability in the details. Many tundra elements were shuffled into the northern fauna and flora and many southern steppic species came into the south. Yet the cold aridity of the openness probably retained much of the same impressionistic character—low sward species, a sea of light green in summer and tan in winter occupied by many of the same species of nomadic or very wide-ranging large mammals—bison, horse, woolly rhino, reindeer, saiga, lion, wolf, spotted hyena and woolly mammoth in particular. Woolly mammoth fossils from Scandinavia with dates ranging from 22,420 ± 315 to 31,970 ± 950 bp (Ukkonen *et al.* 1999; Larsson, this volume) and from the northern Russian locality Byzovaya (65° N) (Pavlov and Indrelid, this volume) support this image.

10. Summary

Ecological and climatological research of the Mid Upper Palaeolithic indicates that the climate of that episode was very unstable, oscillating around a set-point that was neither comparable to that of the Holocene nor to that of the Last Glacial Maximum. Fluctuations in the Atlantic current, jet stream shifts or other factors resulted in short, infrequent saw-tooth climatic switches, with episodes characterised by a higher frequency of clear skies, resulting in arid summers and cold winters. The duration of these oscillations was too short to re-arrange the palaeoenvironment completely as biotic changes require some lag time, thereby weakening the impact of the climatic switches and maintaining a mean climate, which was neither warm and moist nor cold and arid.

The environment from Western Europe to Alaska was remarkably uniform and generally open toward steppic. The fossil floral and faunal communities from this large area show a 'no-modern-analogue', as evidenced by the coexistence of species which do not have an overlap today, as we know from the Mammoth Steppe. It is, with its rich biodiversity, however, a less intense version of the Mammoth Steppe. An environment with a relatively high biomass of larger mammals, mainly nomadic, wide-ranging large herbivores such as woolly mammoth, bison, horse, woolly rhino, reindeer and saiga; an environment with large herds providing considerable opportunity for large mammal hunting specialists, including humans.

references

- An, Z.S.,
D.H. Sun,
X.Y. Zang,
W.J. Zhou,
S.C. Porter,
J. Shaw,
D.Z. Zang
- 1995 Accumulation sequence of Chinese loess and climatic records of Greenland ice core during the last 130 ky, *Chinese Science Bulletin* 40, 1272-1276.
- Ballantyne, C.K.,
C. Harris
- 1994 *The periglacial of Great Britain*. Cambridge: Cambridge University Press.
- Bartlein, P.J.,
P.M. Anderson,
M.E. Edwards,
P.F. McDowell
- 1991 A framework for interpreting paleoclimatic variations in eastern Beringia, *Quaternary International* 10-11, 73-83.
- Berger, A.
- 1978 Long-term variations of daily insolation and Quaternary climate changes, *Journal Atmospheric Sciences* 35, 2362-2367.
- Berman, D.I.,
A.V. Alfimov
- 1997 *The Bering 'Bridges' during the Pleistocene according to the point of view of migrating invertebrates*. Abs. Beringian Paleoenvironments Workshop, 32-33, Florissant Colorado, September 20-23, 1997.
- Bond, G.,
W. Broecker,
S. Johnson,
J. McManus,
L. Labeyrie,
J. Jouzel,
G. Bonani
- 1993 Correlations between climate records from North-Atlantic sediments and Greenland ice, *Nature* 365, 143-147.
- Chen, F.H.,
J. Bloemendal,
J.M. Wang,
J.J. Li,
F. Oldfield
- 1997 High-resolution multi-proxy climate records from Chinese loess: evidence for rapid climatic changes over the last 75 kyr, *Palaeoogeogr., Palaoclimatol., Palaeoecol.* 130, 323-335.
- Colinvaux, P.A.,
F.H. West
- 1984 The Beringian Ecosystem, *Quarterly Review of Archaeology* 7, 8-9.
- Cwynar, L.C.,
J.C. Ritchie
- 1980 Arctic Steppe-Tundra: a Yukon perspective, *Science* 208, 1375-1378.
- Davis, M.B.
- 1981 Quaternary history and the stability of forest communities. In: D.C. West, H.H. Shugart and D.B. Botkin (eds), *Forest succession: concepts and applications*, 132-153, New York: Springer.
- DeMenocal, P.B.,
D. Rind
- 1993 Sensitivity of Asian and African climate to variations in seasonal insolation, glacial ice cover, sea surface temperature, and Asian orography, *Journal of Geophysical Research* 98, 7265-7297.
- Ding, Z.L.,
N. Rutter,
J.M. Han,
T.S. Liu
- 1992 A coupled environmental system formed about 2.5 Ma in East Asia, *Palaeoogeogr., Palaoclimatol., Palaeoecol.* 94, 223-242.

- GRIP 1993 Climate instability during the last interglacial period recorded in the GRIP ice core, *Nature* 364, 203-207.
- Guthrie, R.D. 1990 *Frozen fauna of the Mammoth Steppe: the story of Blue Babe*. Chicago: University of Chicago Press.
- in press *Origin and causes of the Mammoth Steppe: A story of cloud cover, woolly mammal tooth pits, buckles and inside-out Beringia*.
- Guthrie, R.D.,
A.V. Sher,
R.C. Harington in press *New Saiga antelope dates from Alaska, Canada and Siberia: Their paleological significance*.
- Hopkins, D.M.,
J.V. Matthews,
C.E. Schweger,
S.B. Young (eds) 1982 *Paleoecology of Beringia*. New York: Academic Press.
- Kotilainen, A.T.,
N.J. Shackleton 1995 Rapid climate variability in the North Pacific Ocean during the past 95,000 years, *Nature* 377, 323-326.
- Larsson, L. this volume *Plenty of Mammoths but no humans? Scandinavia during the Middle Weichselian*.
- Markova, A.K.,
N.G. Smimov,
A.V. Kozharinov,
N.E. Kazantseva,
A.N. Simakova,
L.M. Kitaev 1995 Late Pleistocene Distribution and Diversity of mammals in Northern Eurasia, *Paleotologia i Evolucia* 28-29, 5-143.
- Manabe, S.,
T.B. Terpstra 1974 The effects of mountains on the general circulation of atmosphere as identified by numerical experiments, *Journal of Atmospheric Science* 31, 3-42.
- Partridge, T.C.,
G.C. Bond,
C.J.H. Hartnady,
P.B. DeMenocal,
W.F. Ruddiman 1995 Climatic effects of the late Neogene tectonism and volcanism. In: E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Buckle (eds), *Paleoclimate and evolution-with emphasis on human origins*, 8-23, New Haven: Yale University Press.
- Pavlov, P.Yu.,
S. Indrelid, this volume *Human occupation of Northeastern Europe during the period 35,000-18,000 bp*.
- Pettitt, P. this volume *Chronology of the Mid Upper Palaeolithic: the radiocarbon evidence*.
- Porter, S.C.,
Z.S. An 1995 Correlation between climate events in the North-Atlantic and China during last glaciation, *Nature* 375, 305-308.
- Roebroeks, W. this volume *A marginal matter: the human occupation of Northwestern Europe – 30,000 to 20,000 years bp*.
- Ruddiman, W.F.,
Kutzbach, J.E. 1989 Forcing of Late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American West, *Journal of Geophysical Research* 94, 18379-18391.
- Shackleton, N.J. 1987 Oxygen isotopes, ice volume and sea-level, *Quaternary Science Reviews* 6, 183-190.

- Sher, A.V. 1968 Fossil saiga in northeastern Siberia and Alaska, *International Geology Review* 10, 1247-1260.
- Soffer, O., 1990 *The World at 18 000 BP. Vol. 1. High Latitudes*. London: Unwin Hyman.
C. Gamble
- Street, M., this volume *The German Upper Palaeolithic 35,000-15,000 bp. New dates and insights with emphasis on the Rhineland*.
T. Terberger
- Storch, G. 1969 Über Kleinsäuger der Tundra und Steppe in jungeszeitlichen Eulengewöllen aus dem nordhessischen LöB, *Natur und Museum* 99, 541-551.
- Stuart, A.J. 1982 *Pleistocene vertebrates in the British Isles*. London: Longman.
- Ukkonen, P., 1999 New radiocarbon dates from Finnish mammoths indicating large ice-free areas in Fennoscandia during the Middle Weichselian, *Journal of Quaternary Science* 14, 711-714.
J.P. Lunkka,
H. Jungner,
J. Donner
- Van Andel, T.H., 1996 Paleolithic landscapes of Europe and environs, 150,000-25,000 years ago: an overview, *Quaternary Science Reviews* 15, 481-500.
P.C. Tzedakis
- Van Cleve, K., 1983 Tundra ecosystems in interior Alaska, *BioScience* 41, 78-88.
C.T. Dryness,
L.A. Viereck,
J. Fox,
F.S. Chapin III,
W.C. Oechel
- Van Kolfschoten, T. 1995 On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe, *Acta zool. Cracov* 38(1), 73-84.
- Van Kolfschoten, T., in prep *The smaller mammals from the Late Pleistocene sequence of the Sesselfels Cave*.
J. Richter Quartärbibliothek.
- Vrba, E.S., 1995 *Paleoclimate and evolution-with emphasis on human origins*. New Haven: Yale University Press.
G.H. Denton,
T.C. Partridge,
L.H. Buckle (eds)
- Wessler, S.D., 1991 Species distribution controls across a forest-steppe transition: a causal model and experimental test, *Ecological Monographs* 6, 323-342.
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